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Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery

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Abstract

Sandeels are small pelagic fish which play an important role in the diet of a range of natural predators. Due to their low occurrence in traditional survey gear, little is known about their large scale distribution or the degree of mixing between habitat areas. We used detailed information collected directly from the fishery to map fishing grounds and assumed these to reflect the foraging habitat of sandeel. Length distributions from individual hauls were used to assess differences in length distributions as a function of the distance between samples. Sandeel foraging habitat covered approximately 5% of the total area of the North Sea. Mixing between neighbouring fishing grounds was too low to eliminate differences in length distributions at distances between grounds down to 5 km. Within fishing grounds, mixing was sufficient to eliminate differences in length distributions at scales less than 28 km but insufficient at greater distances. The lack of mixing between grounds may result in large differences in sandeel abundance among adjacent fishing grounds. Further, high abundance at one end of a large fishing ground is not necessarily indicative of high abundance at the other end.

Key words

Fishery cooperation, habitat mapping, sandeel, scale of mixing

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Introduction

Sandeels (*Ammodytes* spp.) are small semi pelagic fish with a worldwide distribution (Smith and Heemstra, 1986). They usually constitute a high proportion of the fish biomass in the regions where they occur (see e.g. Reay, 1970), and are an important prey species for numerous fish, seabirds and mammals (Daan, 1989; Furness, 1990; Wanless *et al.*, 1998). In addition, they are the target of a large scale industrial fishery in the North Sea (ICES, 2008a). This has led to concerns as to whether fisheries pose a threat to top predators through their reduction of the food supply (Macer, 1966; Monaghan, 1992; Wright, 1996; Wanless *et al.*, 1998; Engelhard *et al.*, 2008). Most sandeel species inhabit shallow, turbulent sandy areas, located on depths between 20 and 70 m where the content of the finest particles silt and clay is low (Macer, 1966; Reay, 1970; Wright *et al.*, 2000). Because of the limited availability of such substrate (Wright *et al.*, 1998), the distribution of post-settled sandeels is highly patchy (Macer, 1966; Wright *et al.*, 2000; Freeman *et al.*, 2004; Holland *et al.*, 2005). Post-settled sandeels are rarely found further than 15 km away from known habitat (Wright, 1996; Engelhard *et al.*, 2008) and the maximum distance travelled by tagged individuals displaced from grounds was 64 km (Gauld, 1990). This lack of large scale dispersal combined with a limited larval exchange between areas (Proctor *et al*., 1999; Christensen *et al*., 2009) means that local aggregations may be vulnerable to depletion by the fishery and increases the risk of adverse effects on local predators even if the North Sea stock is inside biologically safe limits. Unfortunately, the lack of knowledge on the location of the majority of these aggregations in the North Sea and the population dynamics within them has hindered studies of local depletion except in a few local areas (Wright, 1996; Rindorf *et al*., 2000; Daunt *et al*., 2008; Engelhard *et al*., 2008).

There are several reasons for the limited knowledge of sandeel distribution and population dynamics. Firstly, sandeel bury into the sediment when not feeding in the water column or when approached by predators foraging near the seabed (Winslade, 1974a,b,c; Girsa and Danilov, 1976; Pearson *et al.*, 1984; Pinto *et al.*, 1984). This burying behaviour makes their accessibility to sampling in the water column highly variable. Due to this variability and the patchy distribution of habitat, none of the regular North Sea acoustic or trawl surveys provide reliable means of mapping sandeel distribution, although both approaches have been used to investigate density in a few areas of the North Sea (Greenstreet *et al*. 2006, ICES 2008b, Johnsen *et al*. 2009). Secondly, although the requirement for specific habitats is likely to limit sandeel movement, little direct information exists on the extent of horizontal movements of post-settled sandeels within or between habitat areas. The few mark-recapture experiments that have been conducted were restricted to small regions because of the difficulty of marking a representative number of this abundant species. Furthermore, the recapture location could not be determined since the species is not sorted onboard fishing boats (Gauld, 1990). Consequently, the distribution of habitat areas must be derived from non-conventional methods and movements of this species throughout a large region such as the North Sea must be assessed from indirect methods.

Movements between habitat areas may be detected by differences between length distributions. Local differences in recruitment, growth or mortality will result in differences between areas unless fish mix between different areas. If differences arise from variation in recruitment between areas, subsequent mixing would lead to a decrease in the difference between length distributions over the season. Alternatively, increasing differences in length distributions over the season could result from variation in growth or mortality and lack of mixing between adjacent areas during the season. This increase should be greater the longer the distance between the habitat areas if growth and mortality differences increase with distance. Alternatively, if mixing occurs at small scales while growth and mortality varies independently of distance, differences between length distributions should increase at small distances but vary independently of distance at large scales. Based on the extent of identified sandeel aggregations (Freeman *et al*., 2004; Holland *et al*., 2005) and the apparent limited movements of settled sandeels it is possible that mixing could be limited both within as well as among habitat areas.

The determination of length distributions in local aggregations repeatedly over a longer period of time is a costly exercise if scientific vessels are required to sample the fish. However, the sandeel fishery could potentially provide crucial information at comparatively low costs. The fishery targets foraging sandeel near areas where the sandeels bury and the fishing grounds should therefore provide information on the distribution of sandeel habitat areas (Jensen 2001). Recognizing that information on sandeel habitat areas was crucial to the validity of the scientific advice given, a collaboration between the Danish Fishermen's Association and the Danish Institute for Fisheries Research, now Danish Technical University, was started in 1999 in order to provide the information needed to improve the understanding of North Sea sandeel population dynamics. Under this collaboration, data were collected by Danish sandeel skippers directly from the fishing vessels.

The objective of this study was to use the detailed data collected in the fishery to produce a map of the foraging habitat of sandeel and then examine the extent of mixing between and within foraging habitats. Foraging habitats are defined here as areas with potential large densities of non-buried sandeel as sandeel bury when not feeding (Winslade, 1974a). Four predictions were made of the relationship between the difference in length distributions and distance between samples in time and space and the extent of mixing:

1) If the difference between length distributions increases with distance *within* a fishing ground, the degree of mixing between subareas of the fishing ground must be limited.

2) If the difference between length distributions increases with distance *between* fishing grounds, the degree of mixing between fishing grounds must be limited.

3) If the difference between length distributions *decreases* over the season, initial differences caused by differences in e.g. recruitment slowly disappear through mixing of fish.

4) If the difference between length distributions *increases* over the season, initial differences are enhanced through changes in growth, mortality or emergence behaviour and lack of mixing.

In both 1) and 2), the distance at which length distributions become significantly different indicates the distance at which the rate of mixing becomes too low to compensate for differences in recruitment, growth and mortality.

Methods

Sandeel foraging habitat

Three types of information were combined to derive the spatial distribution of foraging habitat: global positioning system (GPS) loggings from individual ships, vessel montiroring system (VMS) data and evaluation of maps by fishermen. GPS based computer systems are used by the fishermen together with information from sea charts and past experience to map and log fishing grounds and fishing activities. The maps contain data on longitude and latitude, and, in some cases, names of the fishing grounds. This detailed information was used to map about 10% of the grounds. To supplement this data, information about catches of sandeel in individual trawl hauls for which the latitude and longitude of hauling were known were used to locate another 50% of the grounds. The remaining 40% of the fishing grounds were obtained from VMS data from Danish vessels fishing sandeel. These data are logged continually while the vessel is at sea. This means that the time not spend fishing for sandeel is included and must subsequently be excluded through filtering. These filtering routines were based on distance between succeeding sample points/positions and additional information collected from Danish fishermen on the physical characteristics (i.e. depth and seabed type etc.) of each fishing ground and the time of the year the ground is usually fished.

From the data collected, the final map of the sandeel fishing grounds was produced using ArcMap and the Spatial Analyst extension (ESRI ArcGIS)(see supplementary material S1). Each fishing ground is defined as a polygon, adjusted manually considering raw data, information about individual grounds, the location of fishing tracks and information about topography. During this process the highest weight was given to the information in the raw data. Fishermen from different harbours evaluated the map of fishing grounds, after which it was modified according to the guidelines given by the fishermen. The evaluation by the fishermen resulted in the inclusion of additional grounds (from additional navigation data) and deletion of non sandeel grounds. The map was subject to several such evaluations before being finalized.

Length distributions of sandeels

From 1999 to 2008, Skippers from 55 sandeel fishing vessels have collected detailed haul information on 2774 individual trawl hauls. Each fishing vessel records information about the exact location and time of shooting and hauling of the trawl, the name of the fishing ground, and an estimate of the total weight of the catch in each individual trawl haul. Further, a sample of between 0.5 and 1 kg fish is collected from each haul and frozen on board. In the laboratory, the sampled fish are thawed, the sandeel are sorted by species, and total length of all fish is measured to nearest half cm below. Samples where less than 50 fish were measured were excluded due to the low accuracy of length distributions based on small samples. Further, as the objective was to compare length distributions between sites, hauls with more than 50 km between start and end positions and hauls with a distance greater than 25% of the length of the fishing ground were excluded.

To derive an estimate of the variation in length distributions within and between fishing grounds while accounting for the unbalanced sampling of weeks and vessels, length distributions were analyzed using generalized linear models of continuation-ratio logits (Rindorf and Lewy, 2001; Marques *et al*., 2005). This method allows statistical testing of the effect of both continuous and discrete variables. Further, by utilizing the smoothness of length distributions as a function of length this method provides more accurate estimates of length distributions than traditional methods (Rindorf and Lewy, 2001). The observations analyzed were distributions of observed lengths in half cm for each of the hauls sampled. They were modelled by fitting fifth degree polynomials to the continuation-ratio-logits (Rindorf and Lewy, 2001).

All models were fitted using the SAS® GENMOD procedure (SAS® version 9.1 for Windows; SAS® Institute Inc. 2004). The dispersion parameter was estimated by Pearson's χ^2 statistic divided by the degrees of freedom. Only length groups with at least one sandeel on average in a sample were included in tests.

Within fishing ground variation

To examine whether length distributions differed within fishing grounds, fishing grounds where more than 20 samples were taken in a 2-week period in a given year were selected. This resulted in seven combinations of fishing ground and time. These fishing grounds were then divided into four parts. North-south oriented fishing grounds were divided according to latitude whereas east-west oriented grounds were divided according to longitude. Individual trawl hauls were then attributed to each of these subareas based on the midpoints between the shooting and hauling positions. Of the fishing grounds selected, Scooter Plads had hauls all originating in the same quarter of the fishing ground and for this fishing ground, this quarter of the fishing ground was divided into two.

The statistical difference between subareas of a fishing ground was estimated using F-tests to compare the deviance of a common length distribution to that of separate length distributions in different subareas (Rindorf and Lewy, 2001), still using fifth degree polynomials to model length distributions. Fishing grounds were analyzed separately to assure that the values obtained were independent. From the F-test, a value of F and a probability of this value at the given number of degrees of freedom are obtained. If the number of degrees of freedom is unaltered, a larger value of F signifies greater difference between samples.

Between fishing ground variation

To examine whether length distributions differed between fishing grounds, grounds where more than five samples were taken in a 2-week period were selected. The distances between all hauls were computed and for each pair of fishing grounds in a 2-week period, the hauls were grouped in bins of 10 km-distance between hauls. Haul pairs from the same fishing ground or hauls more than 75 km apart were excluded. Two models were then fitted for each combination of fishing grounds and distance using the method described in the previous section: one modelled a common length distribution and the other modelled two length distributions, one for each fishing ground. From the residual deviances, the F-value of assuming a common length distribution was estimated along with the probability of this value. This resulted in a list (cleaned for doublets) of name of fishing ground 1, name of fishing ground 2, distance-group (10 km groups), F-values and the probability of all samples being derived from a common length distribution.

Trends over time

To examine whether the difference between length distributions generally decreased or increased over time, the correlations between F of the between fishing ground comparison and week of the year were estimated for each distance-group. Only groups where three or more 2-week-periods were sampled in the main fishing season (week 14 to 22) were included.

Results

Sandeel foraging habitat

A total 217 individual habitat areas were identified with a total area of 33 566 km^2 equivalent to approximately 5% of the area of the North Sea and Skagerrak (Figure 1). The habitat areas vary greatly in size as the area ranges from 1 km^2 to 4023 km^2 (Figure 2). Given the average estimated biomass of sandeel in the North Sea (ICES 2008a), this leads to a density within habitat areas of on average 58 ton per km^2. With an average weight of sandeel of 7 g (ICES 2008a), this corresponds to eight sandeels per m^2 habitat.

Within fishing ground variation

Length distributions of sandeels from 187 hauls taken at five fishing grounds were used (Figure 1). Of these fishing grounds, the number of samples taken exceeded 20 in two consecutive 2-week periods on two of them. It is clear from visual inspections of the length distributions that the variation between fishing grounds is much larger than the within fishing ground variation (Figure 3). The length distributions differed significantly between subareas of the fishing ground on two fishing grounds (a total of three cases, Table 1, Figure 4) and the difference increased significantly with length of the fishing ground (correlation between F and distance between outer subarea midpoints=0.86, P=0.0135). The regression line exceeded an F-value of two (roughly equal to a difference significant at the 5% level when the number of degrees of freedom is large) at a minimum distance between subareas of 28 km (Figure 5). At smaller distances, the length distributions were not significantly different and hence mixing most likely occurred at these scales. As the distance refers to the distance between fishing ground subarea centres and subareas are defined as quarters of fishing grounds, this corresponds to a total mixing of fish at fishing grounds of lengths less than 112 km.

Between fishing ground variation

The length distributions differed significantly between fishing grounds in a total of 55 cases (90%). Length distributions of sandeels from 1038 hauls taken at 11 fishing grounds were used, resulting in a total of 61 combinations of fishing ground pair and 10 km distance group (see Supplementary material S2). The F-value of the difference between length distributions increased significantly with distance between fishing grounds (correlation between F and distance group=0.30, P=0.0184)(Figure 6a) and the regression line exceeded an F-value of two at a minimum distance between fishing grounds of 5 km. The difference between length distributions was substantially higher between fishing grounds than within fishing grounds even at the same geographical distance (Figure 6b). Whereas within-fishing ground comparisons did not reveal significant differences at distances below 40 km (Figure 5), all of the between-fishing ground comparisons made at distances less than 20 km (total of three) and all but one made at distances of less than 30 km (total of 10) were significantly different (Figure 7).

Trends over time

None of the correlations between F and week were significant at the 5% level when performed separately for each distance group and hence differences did not increase or decrease significantly over time at a given distance. However, the correlation between F and week within a distance group increased significantly with distance (Pearson correlation coefficient=0.93, P=0.0211)(Figure 8). This indicates that there was no tendency for nearby grounds to become more similar over time (correlation between F and time was zero) while distant grounds became more different over time (F between distant grounds increased over time).

Discussion

This study utilized the first North Sea wide map of lesser sandeel distribution to evaluate dynamics over a complex mosaic of grounds differing widely in size and proximity to each other. The mixing of sandeel between these grounds was insufficient to eliminate significant differences in length distributions at spatial scales down to 5 km. Within grounds, the mixing is greater and at fishing grounds with a length smaller than 112 km, no difference in length distributions was found. However, beyond this distance, the mixing was again insufficient to eliminate differences in length distributions. This lead to increased differences between fishing grounds late in the season as differences in growth and mortality enhanced early season differences. The lack of mixing between fishing grounds potentially increases the risk of adverse effects of the fishery on local predators even if the population at a larger scale is inside biologically safe limits.

The validity of the map as an indicator of sandeel foraging habitat depends on whether all habitat areas are known and fished by the fishery and whether fishing is restricted to foraging areas. Comparison with smaller scale topographical and benthic mapping suggests that the fishery tends to concentrate in areas where sandeel forage, which often coincide with the edge of fishing grounds (Jensen, 2001; Holland *et al*., 2005; Mackinson and van der Kooij, 2006; Engelhard *et al*., 2008). Given the close proximity between foraging habitat and preferred substrate, fishing distribution should provide a good proxy for areas of sandeel habitat (Wright *et al*., 2000; Van der Kooij *et al*., 2008). However, vessels only fish in areas with clear tows and a high catch rate and avoid shallow waters as well as areas within the territorial limits of countries other than Denmark. Hence, rugged and coastal habitat may be underrepresented in the map. The majority of the catch from coastal habitats is, however, likely to consist of the more coastal sandeel species *Ammodytes tobianus* (Jensen *et al.* 2004).

We are not aware of any similar investigations where mixing has been deduced from comparisons of length distributions. There may be several reasons for this. Firstly, comparisons of length distributions is not straight forward when the number of fish measured is limited (Rindorf and Lewy, 2001). Secondly, a difference in length distributions is not equivocal as this may be caused either by lack of mixing and highly variable growth and mortality rates or by size-dependent migration where fish migrate to specific areas when they reach a certain size. Similarly, identical length distributions may be a result of identical recruitment, growth and mortality patterns combined with a lack of mixing. The lack of difference in length distribution seen within small fishing grounds is therefore not necessarily a result of mixing but could be a result of homogeneous recruitment pattern combined with low differences in growth and mortality rates. However, as one subarea of the fishing ground did not consistently hold larger fish in the fishing ground sampled in two consecutive 2-week periods (Figure 4), it seems unlikely that size dependent migration is the cause of the difference in length distributions between fishing ground subareas. Furthermore, it seems unlikely that such size dependent migration should be larger between fishing grounds than within fishing grounds which would be required to explain the larger differences between grounds. While size-dependent migration may thus occur, it is insufficient to explain the large differences between fishing grounds. This is consistent with the very high recapture rates of tagged sandeels recorded on fished grounds (Kunzlik *et al*., 1986). The recorded differences between length distributions reveal not only lack of extensive movement but also large differences in local recruitment, growth or mortality and possibly also in burying behaviour. Burying behaviour affects the length distribution if the proportion of time spent buried varies between different lengths of sandeel. If this behaviour furthermore varies between fishing grounds, the effect can be increased differences over the season. Significant regional differences in length distribution, growth and maturity have also been found in other studies (Wright, 1996; Bergstad *et al*., 2001; Boulcott *et al*., 2007; Johnsen *et al*., 2009). The present study provides further explanation for this regional variability in dynamics.

In the extreme, local depletion may occur in one end of a large ground while there are high sandeel densities in the other end or at one of two neighbouring fishing grounds. This could be caused by fishing if the fishery remains on the low abundance end of the ground even when density is higher in the other end, a behaviour which would however not appear to maximise profit. The limited exchange between nearby areas potentially increases the effectiveness of closing local areas to fishing as the sandeel inside the area will not simply ‘spill-over’ into adjacent fishing grounds and be caught there. However, the relationship between exchange and differences in local densities were not investigated and hence a ‘spill-over’ effect could potentially occur if there were large density differences between two adjacent areas. In this case, lower competition for food in the low-density area may give sandeel energetic reasons to switch area. Furthermore, the present analysis deals only with mixing in the feeding season. Mature sandeel emerge from the sandbanks in December and January to spawn (Gauld and Hutcheon, 1990; Boulcott *et al*., 2007), and whether mixing takes place during this event is unknown. However, as egg and early larval distributions closely match known overwintering habitat, this appears unlikely (Wright and Bailey, 1996; Munk *et al*., 2002). After hatching, larvae may drift considerable distances (Proctor *et al*., 1998; Christensen *et al*., 2009) and the horizontal movements of pre-settled sandeel (Wright, 1996) most likely leads to exchange of recruits between fishing grounds. Hence, closing a particular fishing ground will protect sandeel during the fishing season and may contribute to recruitment on other fishing grounds but is unlikely to assure the presence of sandeel in the closed fishing ground in coming years.

In conclusion, the distribution of sandeel in the North Sea is highly patchy and there is limited exchange between even close fishing grounds during the fishing season. Some mixing occurs within fishing grounds but the mixing between grounds appears to be very low. Management through closed fishing grounds or fishing ground subareas therefore has the potential to protect local aggregations of sandeel during the fishing season and may result in increased recruitment to nearby fishing grounds, but such a protection is unlikely to assure continuous recruitment to the particular fishing ground.

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Supplementary material

The following supplementary material is available at *ICESJMS* online: Material S1 shows the sandeel map and procedures for its derivation whereas Table S2 lists results of the comparison of length distributions between fishing grounds.

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Table 1. Comparison of length distributions between subareas within fishing grounds. Length indicates maximum distance between midpoints of subareas sampled. Total deviance and df indicates the deviance from a common length distribution and the degrees of freedom of this common length distribution. Subarea deviance indicates the reduction in deviance obtained by modelling the length distribution in each subarea separately and the associated loss of degrees of freedom.

Fishing ground	Length	Total		Subarea			
	(km)	deviance	df	deviance	df	F	P(F)
Scooter Plads	6	830.8	329	22.7	6	1.498	0.1780
Berwick Bank	13	1 191.7	281	46.8	7	1.576	0.1422
Berwick Bank	13	805.3	257	10.9	6	0.580	0.7464
Inner Shoal	25	1 166.3	468	27.2	6	1.819	0.0936
Sorel	41	806.4	307	98.7	10	3.758	0.0001
Elbow Spit	121	1 205.7	337	260.5	15	4.854	<0.0001
Elbow Spit	121	1 635.8	341	336	19	3.686	<0.0001

Captions

Fig. 1. Sandeel habitat areas (areas with potential high density of non-buried sandeel) and named fishing grounds referred to in the text.

Fig. 2. Frequency distribution of area (in km^2) of individual sandeel habitat areas. Lower axis indicates lower limit of 100 km^2-intervals..

Fig. 3. Length distributions at fishing grounds where more than 20 hauls were taken in a 2-week period. a: Scooter Plads (maximum distance between subarea midpoints 6 km), b and c: Berwick bank (maximum distance between subarea midpoints 13 km) week 22 and 24, respectively, d: Inner Shoal (maximum distance between subarea midpoints 25 km), e: Sorel (maximum distance between subarea midpoints 41 km), f and g: Elbow Spit (maximum distance between subarea midpoints 121 km) week 16 and 18, respectively. Colours indicated subarea of fishing ground.

Fig. 4. Length distributions in different subareas. a: Sorel, b: Elbow Spit, week 16, c: Elbow spit week 18. Solid black lines: subarea immediately west of centre, hatched black lines: subarea close to the western end of the fishing ground, solid grey lines: subarea immediately east of centre, hatched grey lines: subarea close to the eastern end of the fishing ground.

Fig. 5. F-value of comparison of common and subarea-specific length distributions as a function of the distance between sampled fishing ground subareas. Line is a regression line.

Fig. 6. F-value of comparison of common and fishing-ground-specific length distributions as a function of the distance between sampled fishing grounds (a) and a

comparison of within and between fishing ground results (b). Line is a regression line. Filled symbols, solid line: between fishing ground comparisons. open symbols, hatched line: within fishing ground comparisons. Note that the values on the y-axis differs between figures as b shows only the lower half of a.

Fig.7. Proportion of analyses showing significant differences as a function of distance. Filled symbols, solid line: between fishing grounds, open symbols, hatched line: within fishing grounds.

Fig. 8. Correlation between week and F for given distance. Positive values indicate a general rise in F over the season, negative a decrease. Line indicates regression line.

Fig. 1.

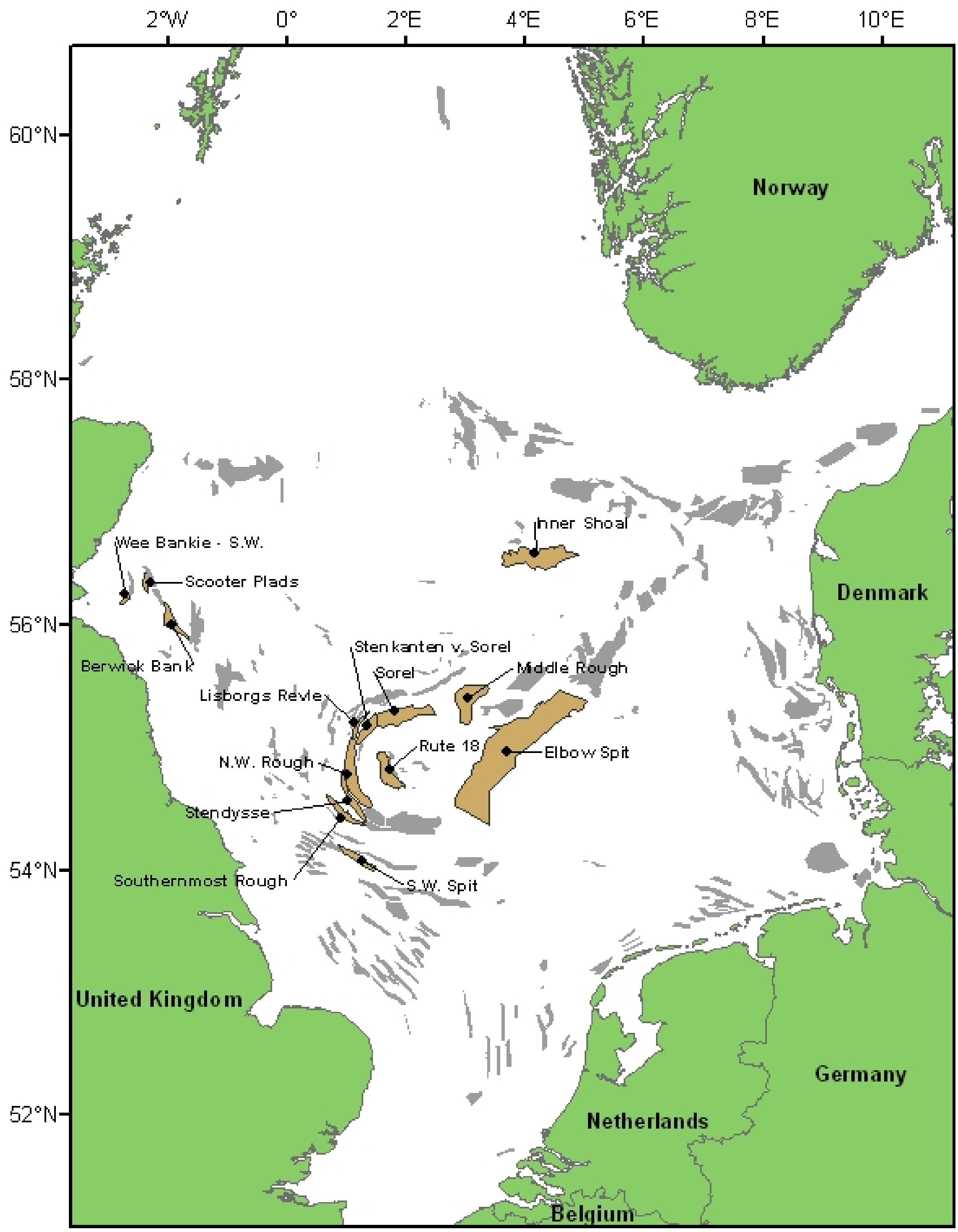

2°W
0°
2°E
4°E
6°E
8°E
10°E
60°N
58°N
56°N
54°N
52°N
Norway
Denmark
United Kingdom
Germany
Netherlands
Belgium
Inner Shoal
Wee Bankie - S.W.
Scooter Plads
Berwick Bank
Stenkanten v. Sorel
Sorel
Middle Rough
Lisborgs Revle
Rute 18
Elbow Spit
N.W. Rough
Stendysse
Southernmost Rough
S.W. Spit

Fig. 2.

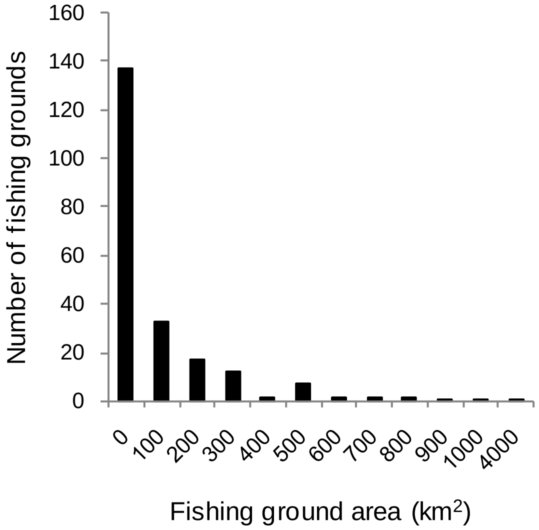

Number of fishing grounds
160
140
120
100
80
60
40
20
0
0
100
200
300
400
500
600
700
800
900
1000
4000
Fishing ground area (km2)

Fig. 3.

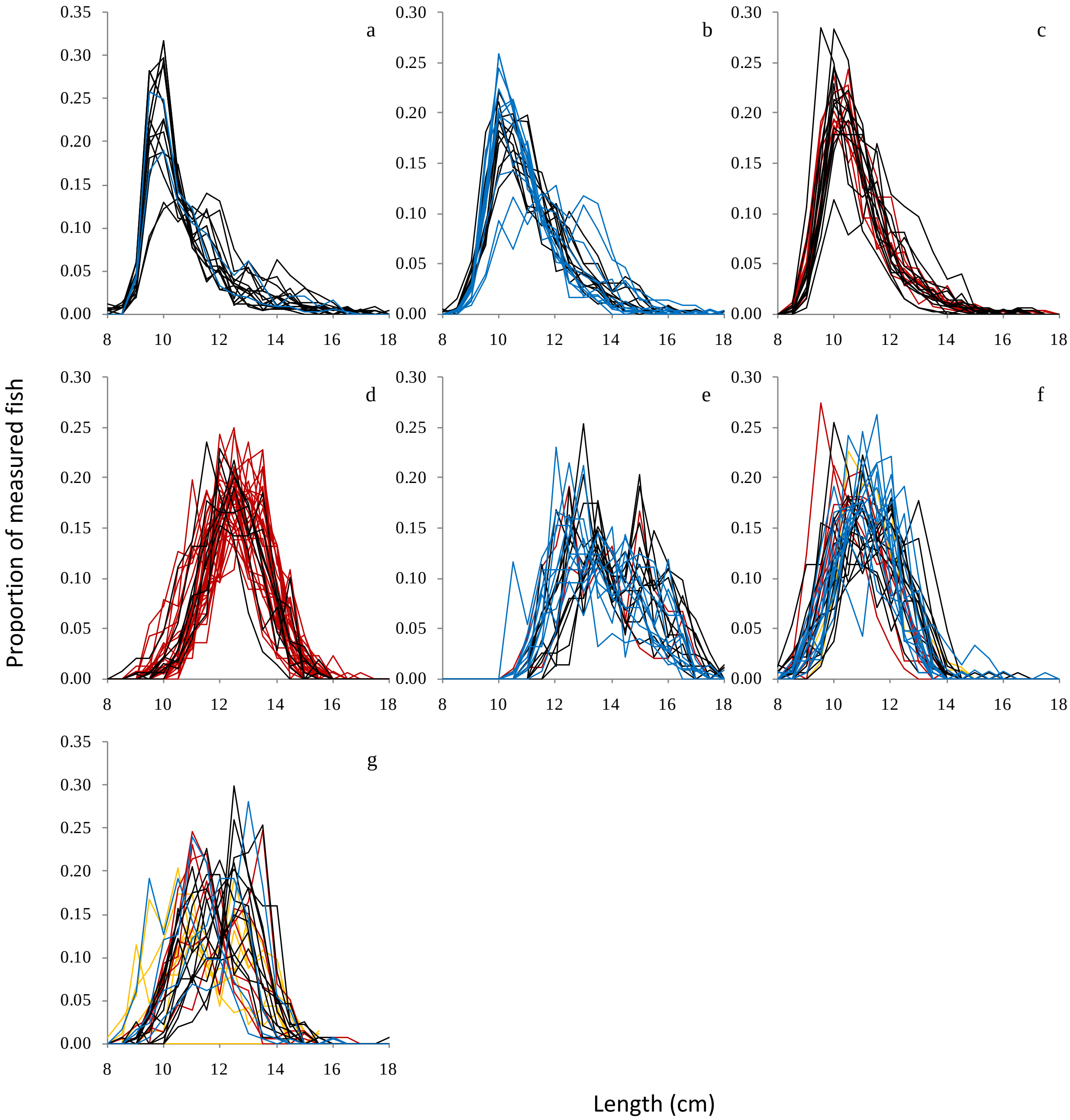
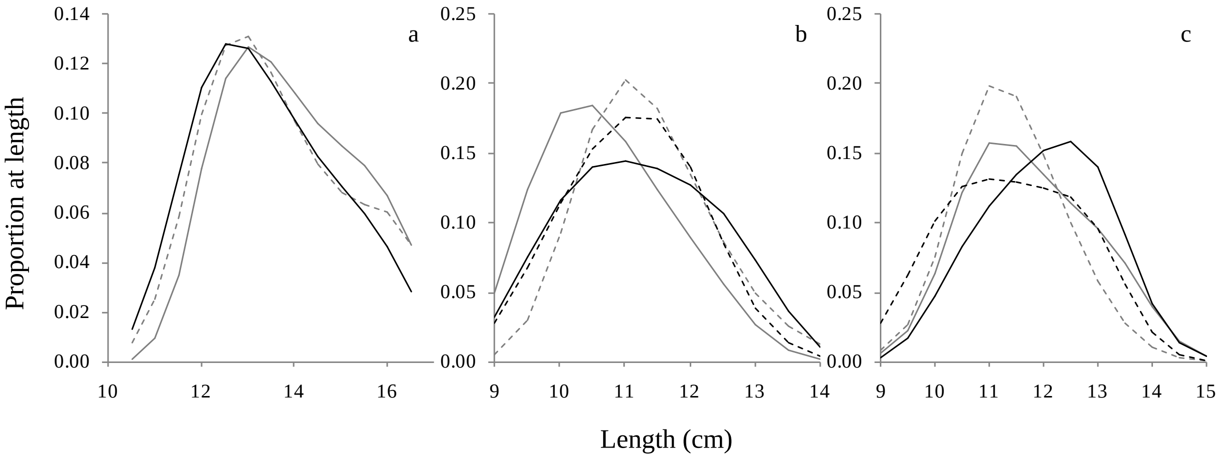
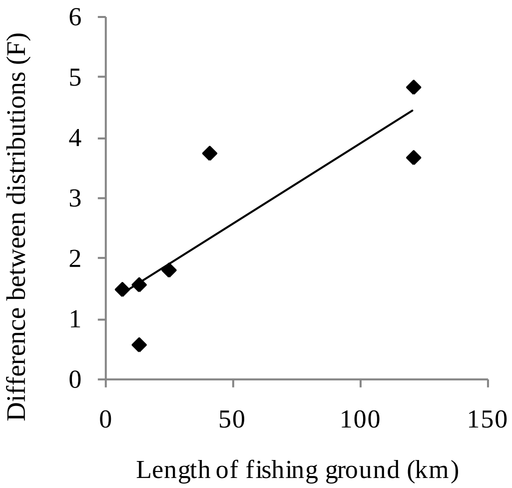

a
b
c
d
e
f
g
Proportion of measured fish
Length (cm)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
8
10
12
14
16
18

Fig. 4.



Proportion at length
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
10
12
14
16
a
0.25
0.20
0.15
0.10
0.05
0.00
9
10
11
12
13
14
b
0.25
0.20
0.15
0.10
0.05
0.00
9
10
11
12
13
14
15
c
Length (cm)

Fig. 5.



Difference between distributions (F)
0
1
2
3
4
5
6
0
50
100
150
Length of fishing ground (km)

Fig. 6.

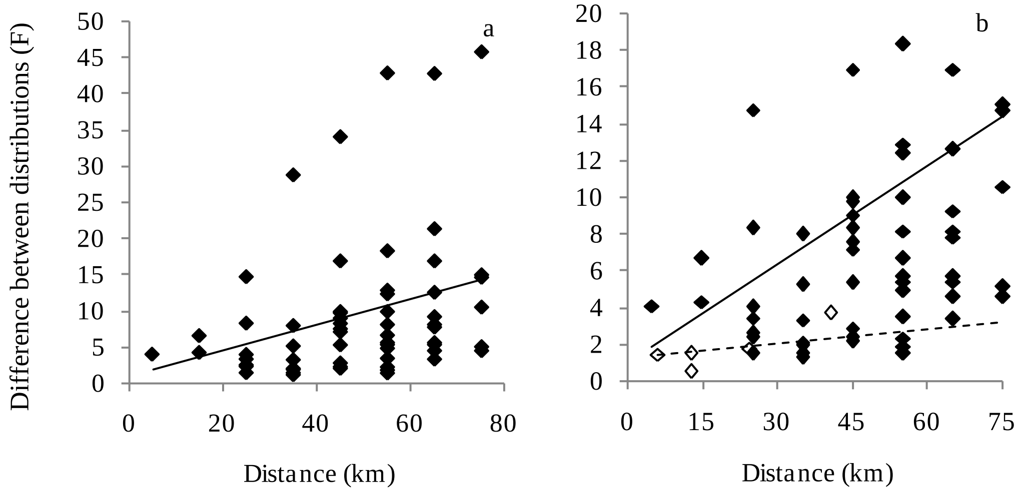

a
b
Difference between distributions (F)
Distance (km)
Distance (km)
0
5
10
15
20
25
30
35
40
45
50
0
20
40
60
80
0
2
4
6
8
10
12
14
16
18
20
0
15
30
45
60
75

Fig. 7.

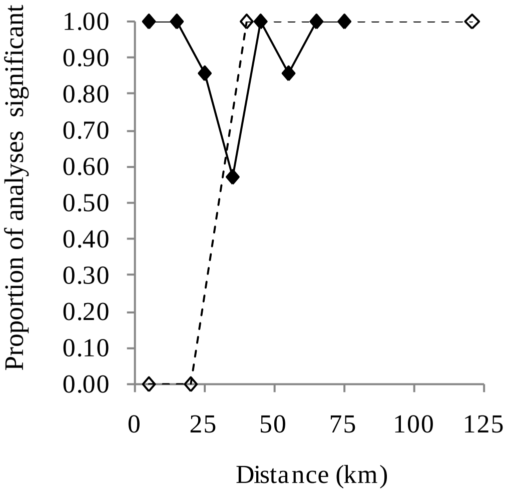
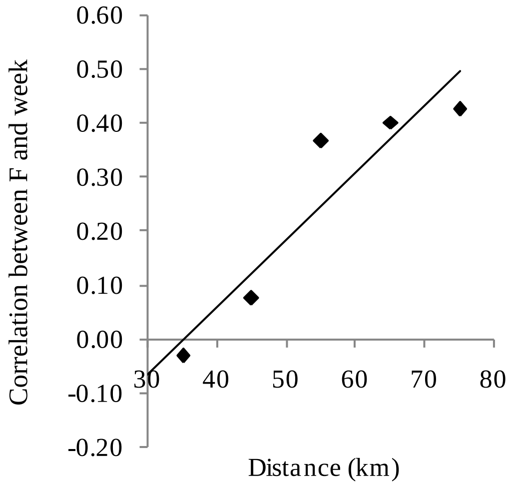

Proportion of analyses significant
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
25
50
75
100
125
Distance (km)

Fig. 8. Correlation between week and F for given distance. Positive values indicate a general rise in F over the season, negative a decrease. Line indicates regression line.



Deriving the map of sandeel habitats (S1)

From the data collected (Figure S1), the final map of the sandeel fishing grounds was produced using the following 5-step procedure:

1) A point shapefile with the data was created from a textfile using ArcMap (ESRI ArcGIS).

2) A kernel density analysis (Silverman, 1986) was applied on the shapefile using a quadratic kernel function to fit a smoothly tapered surface to each point (search radius: 0.015 decimal degrees, output cell size: 0.006 decimal degrees) and produce a grid using the Spatial Analyst extension with ArcGIS .

3) From this grid, a new grid including only cells with a density of points greater than 50 000 was produced. This grid was afterwards converted to a shapefile so that each fishing ground is defined as a polygon.

4) The polygons were adjusted manually considering raw data, information about individual grounds, the location of fishing tracks and information about topography. During this process the highest weight was given to the information in the raw data.

Lastly, fishermen from different harbours evaluated the map of fishing grounds, after which it was modified according to the guidelines given by the fishermen. The evaluation by the fishermen resulted in the inclusion of additional grounds (from additional navigation data) and deletion of non sandeel grounds. The map was subject to several such evaluations before the final map was accepted (Figure S2).

References

Silverman, B.W. 1986. Density Estimation for Statistics and Data Analysis. New York: Chapman and Hall, 175 pp.

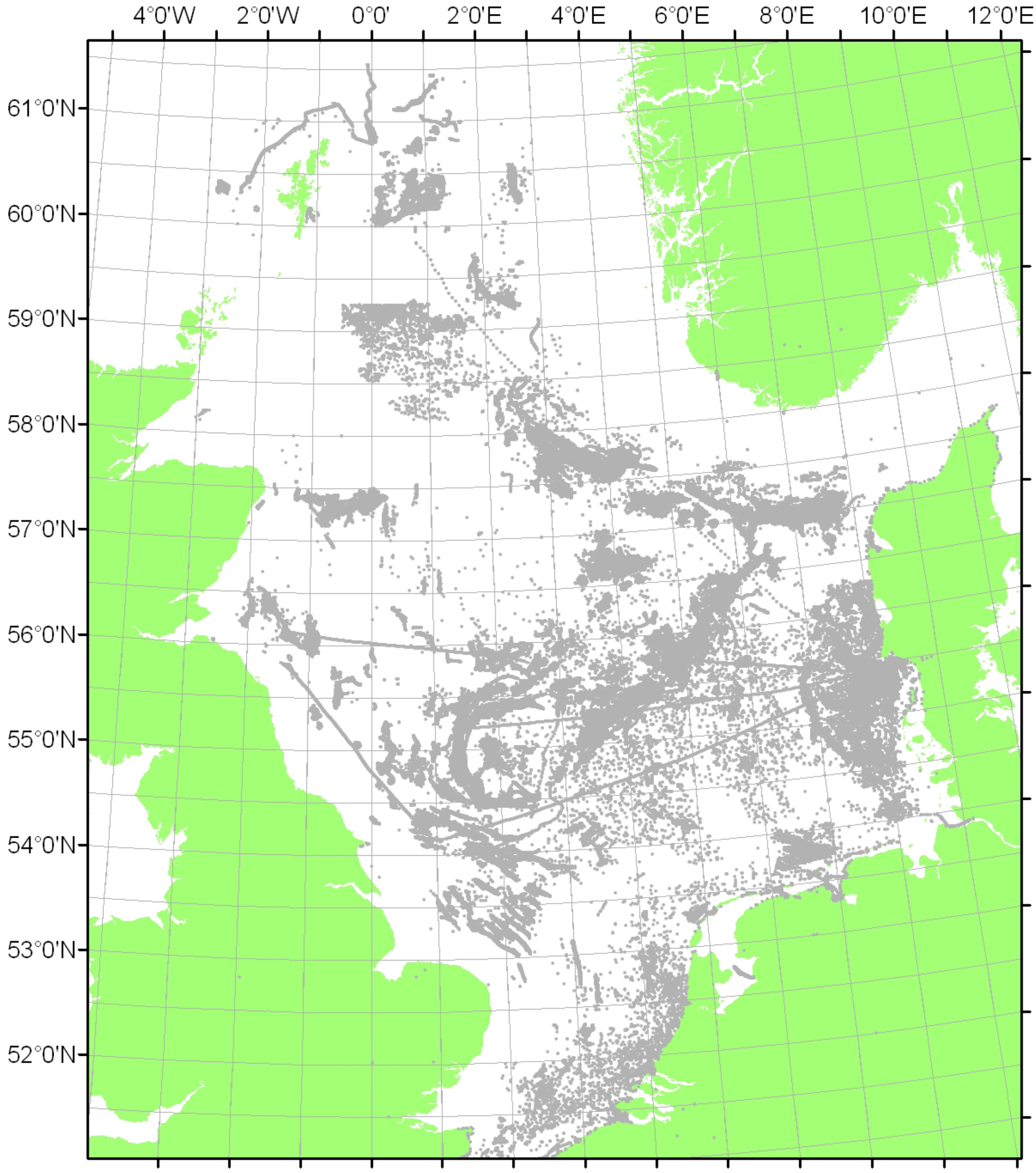


Fig. S1. Map of raw data from various GPS based navigation systems.

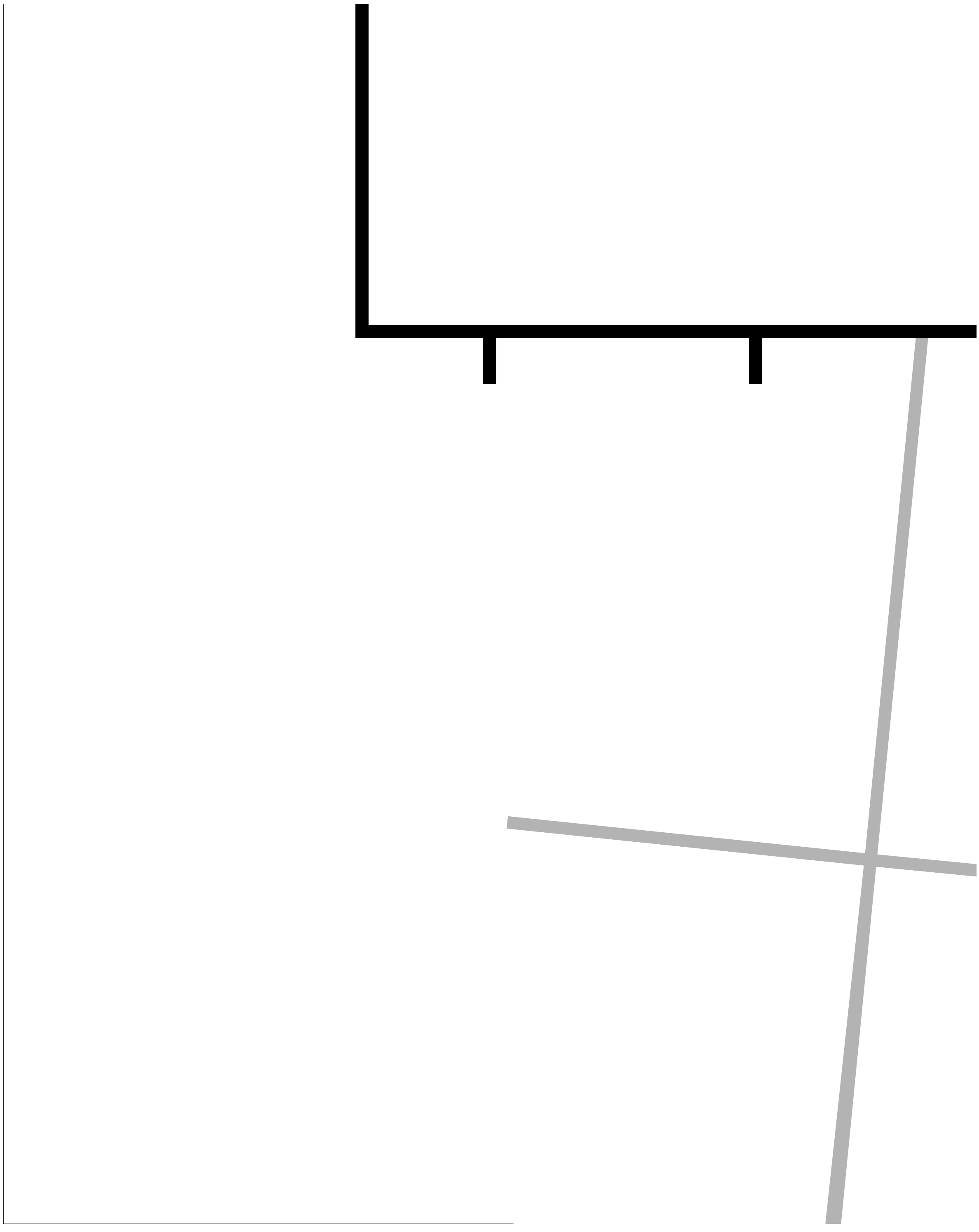


Fig. S2. Sandeel habitat areas.

Table S2. Results of the comparison of length distributions between fishing grounds. Total deviance and df indicates the deviance from a common length distribution and the degrees of freedom of this common length distribution. Ground specific deviance indicates the reduction in deviance obtained by modelling the length-distribution in each area separately and the associated loss of degrees of freedom. Distance groups are 10 km groups denoted by the lowest distance in the group (e.g. 0 equals the group 0-10 km).

			Total		Ground specific			
Ground 1	Ground 2	Distance group	deviance	df	deviance	df	F	P(F)
N.W. Rough	Stendysse/Lissis Revle	0	416	159	52	5	4.11	0.0012
N.W. Rough	Stendysse/Lissis Revle	10	433	174	53	5	4.35	0.0007
N.W. Rough	Stendysse/Lissis Revle	10	1 150	179	249	6	6.67	<0.0001
N.W. Rough	Southernmost Rough	20	430	153	43	6	2.64	0.0159
N.W. Rough	Southernmost Rough	20	995	239	84	6	3.45	0.0022
N.W. Rough	Southernmost Rough	20	1 112	196	81	6	2.45	0.0234
N.W. Rough	Stendysse/Lissis Revle	20	474	160	120	5	8.39	<0.0001
N.W. Rough	Stendysse/Lissis Revle	20	892	228	36	6	1.57	0.1524
Rute 18	N.W. Rough	20	278	129	42	5	4.08	0.0014
Scooter Plads	Wee Bankie - S.W.	20	1 243	382	284	6	14.79	<0.0001
N.W. Rough	Southernmost Rough	30	482	168	56	6	3.36	0.0030
N.W. Rough	Southernmost Rough	30	1 291	259	63	6	2.15	0.0455
N.W. Rough	Southernmost Rough	30	640	186	36	7	1.56	0.1430
N.W. Rough	Stendysse/Lissis Revle	30	736	178	48	6	2.01	0.0614
Rute 18	N.W. Rough	30	522	179	74	5	5.25	0.0001
Sorel	N.W. Rough	30	1 723	255	1 141	6	28.81	<0.0001
Sorel	N.W. Rough	30	791	164	30	5	1.29	0.2664
Sorel	Stenkanten v. Sorel	30	513	204	118	6	8.06	<0.0001

Middle Rough	Sorel	40	679	177	101	5	5.40	0.0001
N.W. Rough	Southernmost Rough	40	557	157	148	6	7.20	<0.0001
N.W. Rough	Southernmost Rough	40	425	153	47	6	2.91	0.0086
N.W. Rough	Southernmost Rough	40	1 447	270	534	6	16.96	<0.0001
N.W. Rough	Southernmost Rough	40	1 937	388	64	6	2.17	0.0432
N.W. Rough	Southernmost Rough	40	1 313	324	272	7	9.81	<0.0001
Rute 18	Stendysse/Lissis Revle	40	617	159	157	5	8.36	<0.0001
Sorel	Lisborgs Revle	40	663	209	185	6	9.99	<0.0001
Sorel	N.W. Rough	40	2 098	313	1 344	6	34.07	<0.0001
Sorel	N.W. Rough	40	849	197	191	6	7.62	<0.0001
Sorel	N.W. Rough	40	985	248	47	5	2.40	0.0356
Sorel	Stenkanten v. Sorel	40	554	218	135	6	9.08	<0.0001
Middle Rough	Sorel	50	1 148	300	234	5	12.42	<0.0001
N.W. Rough	S.W. Spit	50	434	140	63	6	3.56	0.0019
N.W. Rough	Southernmost Rough	50	580	158	143	6	6.74	<0.0001
N.W. Rough	Southernmost Rough	50	425	138	34	6	1.94	0.0736
N.W. Rough	Southernmost Rough	50	1 591	285	424	6	12.93	<0.0001
N.W. Rough	Southernmost Rough	50	1 762	341	72	6	2.36	0.0284
N.W. Rough	Southernmost Rough	50	2 090	394	575	6	18.35	<0.0001
N.W. Rough	Southernmost Rough	50	1 374	236	280	6	8.21	<0.0001
Rute 18	Southernmost Rough	50	618	168	97	5	5.45	0.0001
Sorel	Lisborgs Revle	50	663	209	185	6	9.99	<0.0001
Sorel	N.W. Rough	50	2 873	441	1 652	6	42.85	<0.0001
Sorel	N.W. Rough	50	813	197	138	6	5.73	<0.0001
Sorel	N.W. Rough	50	820	192	32	5	1.53	0.1788
Sorel	Stenkanten v. Sorel	50	382	154	71	6	4.94	0.0001
Middle Rough	Sorel	60	1 110	299	231	5	12.64	<0.0001
N.W. Rough	Southernmost Rough	60	468	130	118	6	5.71	<0.0001
N.W. Rough	Southernmost Rough	60	1 447	270	534	6	16.96	<0.0001
N.W. Rough	Southernmost Rough	60	1 584	291	110	6	3.44	0.0022

N.W. Rough	Southernmost Rough	60	1 996	380	664	6	21.39	<0.0001
N.W. Rough	Southernmost Rough	60	1 374	236	280	6	8.21	<0.0001
Rute 18	Southernmost Rough	60	618	168	97	5	5.45	0.0001
Sorel	Lisborgs Revle	60	527	153	131	5	7.85	<0.0001
Sorel	N.W. Rough	60	2 819	441	1 619	6	42.78	<0.0001
Sorel	N.W. Rough	60	948	232	222	6	9.29	<0.0001
Sorel	N.W. Rough	60	1 181	293	91	5	4.61	0.0004
Middle Rough	Sorel	70	872	230	273	5	14.71	<0.0001
N.W. Rough	Southernmost Rough	70	943	139	493	5	15.05	<0.0001
N.W. Rough	Southernmost Rough	70	986	188	157	6	5.15	<0.0001
Sorel	N.W. Rough	70	2 975	469	1 720	6	45.76	<0.0001
Sorel	N.W. Rough	70	990	244	252	6	10.60	<0.0001
Sorel	N.W. Rough	70	1 181	293	91	5	4.61	0.0004